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Artículo Original

TAXONOMIC NOVELTIES IN *Didelphis albiventris* LUND, 1840 AND REVALIDATION OF *Didelphis poecilotis* A. WAGNER, 1842 (DIDELPHIMORPHIA, DIDELPHIDAE)

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ABSTRACT. In a recent article, we showed that *Didelphis albiventris* might be separated into two taxonomic entities. Molecular evidence, environmental niche modeling, and qualitative morphological characters indicate that there are two clearly separated groups, one including specimens from central and northern Brazil, and the other comprising Argentina, Uruguay, Paraguay, Bolivia, and southern Brazil. In this contribution, we formalize the splitting of the white-eared opossum into two species, *D. albiventris* for the northern group and *D. poecilotis* for the southern group, and we provide an emended diagnosis for both species and information on type specimens and distribution.

RESUMEN. NOVEDADES TAXONÓMICAS EN *Didelphis albiventris* LUND, 1840 Y REVALIDACIÓN DE *Didelphis poecilotis* A. WAGNER, 1842 (DIDELPHIMORPHIA, DIDELPHIDAE). En un artículo reciente demostramos que *Didelphis albiventris* podría separarse en dos entidades taxonómicas. Evidencias moleculares, el modelado del nicho ambiental y diversos caracteres morfológicos indican que existen dos grupos claramente separados, uno que incluye especímenes del centro y norte de Brasil y otro que comprende Argentina, Uruguay, Paraguay, Bolivia y el sur de Brasil. En esta contribución formalizamos la división de la comadreja overa en dos especies, *D. albiventris* para el grupo norte y *D. poecilotis* para el grupo sur y presentamos diagnosis enmendadas para ambas especies e información sobre los ejemplares tipo y su distribución.

Key words: Marsupials, nomenclature, taxonomy, white-eared oposum.

Palabras clave: Comadreja overa, marsupiales, nomenclatura, taxonomía.

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INTRODUCTION

The white-eared opossum, *Didelphis albiventris* Lund, 1840, is a widely distributed marsupial ranging from French Guiana and northeastern Brazil to south-central Argentina (Adler et al. 2006; Astúa 2015; Chemisquy & Martin 2019). As a conspicuous component of the South American mammal fauna, the species has a long history of mentions in the literature. Some of the first records of *Didelphis albiventris* from eastern Brazil and Argentina date back to Sebastian Cabot's conquest and exploration of the area about 1528, as recorded by Herrera y Tordesillas in 1601. The first description of mammals from southern Brazil was attributed to André Thevet by Hershkovitz 1987, who apparently described the locally common opossum (*Didelphis albiventris*). However, the only reference we found in the work of Thevet (1558) provides the following description: "And the said rivers are frequented by a type of animal that the Savages call in their language Saricouienne, which translates to 'dainty animal.' In fact, it is an amphibious creature that spends more time in the water than on land and is no bigger than a small cat. Its fur, patterned with gray, white, and black, is as fine as velvet, and its feet resemble those of a waterfowl. Moreover, its flesh is very delicate and excellent to eat. In this land, there are other very strange and monstrous animals toward the strait, though not as fierce as those in Africa." A footnote (p. 284) added by Paul Gaffarel in his *Nouvelle Édition* of Thevet's work (1878) states: It is the opossum, a mammal of the marsupial order, whose female has under her belly a kind of pouch in which she carries her young. The description provided above aligns more closely with the water opossum (*Chironectes minimus*) than the white-eared opossum (*Didelphis albiventris*). A posterior explorer, Georg Marcgraf, was part of an expedition led by Johann Moritz that landed in Pernambuco around 1630 and explored the northeast of Brazil in the modern states of Pernambuco, Paraiba, and Rio Grande do Norte (Hershkovitz 1987). He arguably wrote the first unequivocal description of *Didelphis* (original in Latin, translated by us with the use of AI), which highlights the white ears typical of this form (marked in bold): *"The Carigueya among the Brazilians, known to some as IVPATIIMA, known as Taiibi in Paraguay (de Lery called it Sarigoy and Ximenes in New Spain called it Tlaquatzin) is an animal resembling a young or medium-sized cat in size: It has a fox-like head, with a pointed mouth, and the lower part of the mouth is slightly shorter than the upper. It has a long tongue, which, however, when the mouth is open, does not protrude threateningly, although it could, but rather raises it towards the back. Its teeth are like those of a cat or a fox, small both in the upper and lower parts, with four long upper canines, indeed longer than the lower ones, and shorter lower ones: indeed sixteen molars, twelve intermediate ones (premolars), four canines, and small incisors in the lower jaw and eight in the upper, for it has two larger ones in the middle like those of a hare. It has open nostrils; beautiful, round, black eyes;* ***ears, proportionate to the size of the body, ample, long, wide, fox-like, which it carries erect, but with thin, translucent membrane lips, translucent whiteness****, with some brownish mix. It has a feline beard with black hairs, but short under the chin, longer in the upper part of the mouth, some above the eyes, and similarly on each cheek." Further in the description of Marcgraf he also mentions the following (apparently taken from Ximenes in his description of America, book V, chapter IV; the bold lettering is ours): "It has a fox-like head, a pointed mouth, a feline beard, prominent and conspicuous black eyes,* ***ears rounded below, soft, slender, white, tender like soft paper"*** (Marcgraf 1648).

Azara (1801, 1802) described six opossums, of which the first one (Micouré premier or El Micuré) clearly corresponds to a white-eared opossum, identified as *D. albiventris* Lund, 1840 (Voss et al. 2009). Based on Hershkovitz (1949) and other sources, Voss et al. (2009) discuss the validity of *D. paraguayensis* Oken (1816), posteriorly resurrected by Allen (1902), and *D. leucotis* Wagner (1847), which are both considered junior synonyms of *D. albiventris*. They also mention the use of *D. azarae* Temmnick, 1824 as considered by Cabrera (1958), but this name applies to black-eared opossums and could represent either a junior synonym of the Amazonian black-eared opossum (*D. marsupialis* Linnaeus, 1758) or a senior synonym of the southeastern Brazilian black-eared opossum (*D. aurita* Wied-Neuwued, 1826) and is not related to *D. albiventris*.

Lemos & Cerqueira (2002) studied white-eared opossums and recognized three morphologically distinguishable groups: *Didelphis albiventris* Lund, 1840, with a distribution from northeastern Brazil to Uruguay, Paraguay, and central Argentina; *D. pernigra* Allen, 1900, with a distribution from western Venezuela to southern Peru; and *D. imperfecta* Mondolfi and Pérez-Hernández, 1984, with a distribution in southeastern Venezuela and northern Brazil.

Recent phylogeographic analyses of mtDNA (COI marker) from *D. albiventris* by Sousa et al. (2012) found two distinct haplogroups, and these authors

proposed that geographic barriers caused these genetic differentiations. Later, Nascimento et al. (2019) added populations from northeastern Brazil to the sample of Sousa et al. (2012), recovering similar results, with populations from Rio Grande do Sul state clearly separated from other Brazilian populations. Rocha et al. (2015) used a different mtDNA genetic marker (cytochrome b), also recovering two haplogroups, one including samples from Paraguay, Bolivia, and the Brazilian state of Paraná, and the other including samples from the Brazilian states of Pará, Tocantins, Mato Grosso, and Minas Gerais. A similar result was reached by Bonvicino et al. (2022), who added more samples to the dataset of Rocha et al., one haplogroup from central Brazil and the other from the Atlantic Shield (i.e., eastern and southern Brazil). Chemisquy et al. (2021) analyzed the phylogeographic structure of populations of *D. albiventris* from Argentina and found evidence for only one haplogroup in the country. In addition, the dataset showed little variation and weak phylogeographic structure.

In a recent article (Chemisquy et al. 2023), we showed that *Didelphis albiventris* might be, in fact, separated into two taxonomic entities. Molecular evidence from two mitochondrial markers indicates that there are two clearly separated groups, one including specimens from central and northern Brazil (haplogroup B), and the other comprising the remaining localities of the species distribution, i.e., Argentina, Uruguay, Paraguay, Bolivia, and southern Brazil (haplogroup A). Apart from the molecular evidence, environmental niche modeling also indicated that each group has a distinctive set of variables defining their climatic niche (Chemisquy et al. 2023). Isothermality and mean diurnal temperature range were the most important variables for the southern group (i.e., haplogroup A), with lower isothermality values (implying higher seasonality) and larger diurnal temperature fluctuations defining its climatic niche. The northern group (i.e., haplogroup B) was characterized by smaller precipitation seasonality and a narrower annual temperature range (Chemisquy et al. 2023: Fig. 7 and Table 3). There are also several qualitative morphological characters differentiating both groups (Chemisquy et al. 2023: Table 2), including cranial (e.g., the posterior portion of the basicranium, the alisphenoid bulla) and dental characters (e.g., the size and shape of the upper premolars, the paracone, and the metacone compared sizes).

DISCUSSION

Based on our interpretation of the genetic results, differences in climatic niches and morphology, which support the existence of two independent evolutionary lineages, we propose to formally split what is currently known as *Didelphis albiventris* into two species: one corresponding to the southern group, distributed in Argentina, Bolivia, Paraguay, Uruguay, and southern Brazil, and the other corresponding to the northern group, distributed in central and northern Brazil (**Fig**. 1).

The type locality of *Didelphis albiventris* is Rio das Velhas, Lagoa Santa, Minas Gerais (Brazil). Although in the previously published article (Chemisquy et al. 2023) we did not include samples from the type locality, we examined several samples from Minas Gerais, some of them located less than 50 km apart from Lagoa Santa, and those samples were clustered in haplogroup B. Consequently, the name *D. albiventris* corresponds to populations from central and northern Brazil (i.e., the northern group). Although Lund (1840) did not mention any specimens, the type of this species, collected by him, is housed in the Natural History Museum of Denmark, consisting of a mounted specimen (catalogued as ZMUC M02-CN4, identified as a syntype; **Fig**. 2), cranium, and postcranial elements (catalogued as ZMUC M02-L4; **Fig**. 2). Examination of photographs of the type specimen (available on GBIF https://www.gbif.org/occurrence/42778687), allowed us to observe some of the characteristics identified for *D. albiventris* in Chemisquy et al. (2023): the shape of the transverse sinus canal and of the alisphenoid portion of the bulla, the direction of the paracondylar process of the exoccipital, and the comparative size and shape of the P3 (**Fig**. 3; also see Chemisquy et al. 2023: Fig. 5 and Fig. 6). Unfortunately, there is no data on the sex of the type specimen nor available measurements, preventing us to provide any further information. We would also like to point out that a specimen identified as a topotype for *D. albiventris* (MN 13414), collected in 1954 by Cory Teixeira de Carvalho in Fazenda do Retiro, Lagoa Santa, Minas Gerais, is housed at the Museu Nacional do Rio de Janeiro (Brazil).

For the southern group, the name that has nomenclatural priority is *Didelphis poecilotis* A. Wagner, 1842, described based on a specimen collected by Johan Natterer (JN 192) in Cuiabá, Mato Grosso, Brazil. The type locality was wrongfully published as Angaba by Wagner (1842), but the specimen comes from Cuiabá according to the catalog of the Naturhistorisches Museum Wien (Frank Zachos pers.

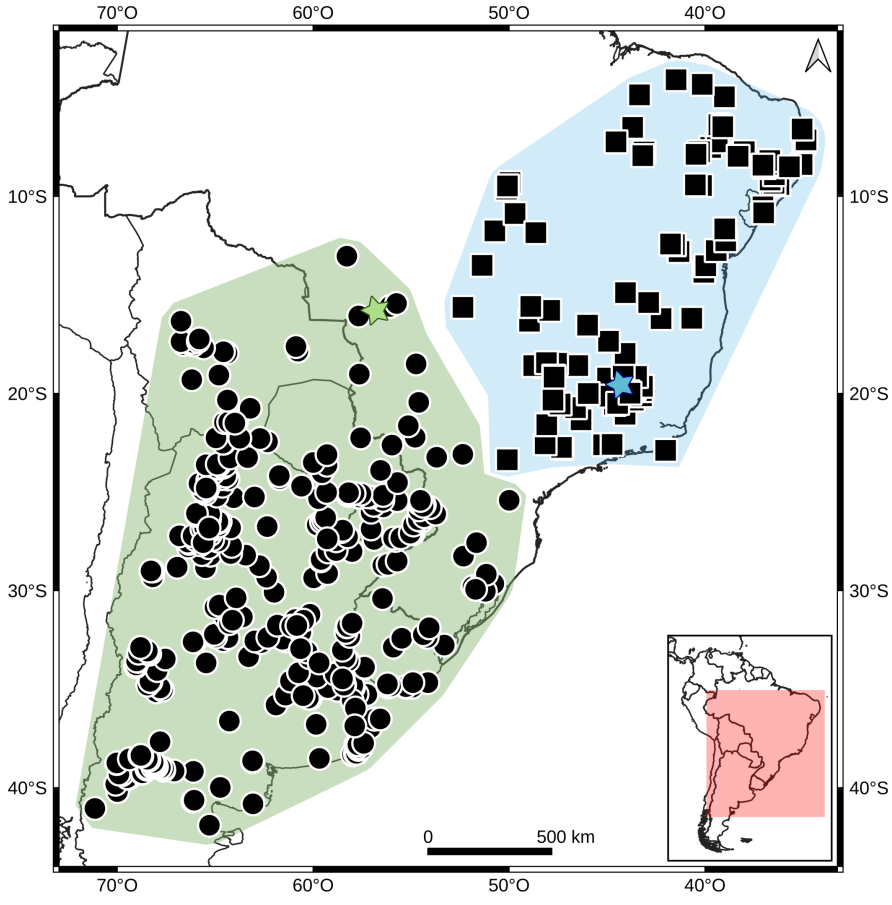

Fig. 1. Geographic separation between *Didelphis albiventris* and *Didelphis poecilotis*. The green shading indicates the schematic geographic distribution of *D. poecilotis*, and the light blue shading the schematic geographic distribution of *D. albiventris*; circles and squares represent specimens that correspond to *D. poecilotis* and *D. albiventris*, respectively. Stars indicate the type localities of both species.

comm., see also von Pelzeln 1883). The type specimen is deposited in the mammal collection of the Naturhistorisches Museum Wien under catalog number NMW ST 54 and consists of a mounted specimen only (an immature female according to the catalog; **Fig**. 4). A second specimen (NMW 1006), also from the Naturhistorisches Museum Wien, was collected by Natterer with Cuyaba as a given locality. However, this one was collected in 1830 and was identified as *D. poecilotis* (with a pencil note stating this). It also states that the only locality where *poecilotis* was found is Cuyaba (probably referring to the only locality where *poecilotis* materials at the NHM were found). It is unclear if the locality "Cuyaba" was inferred from the identification as *poecilotis* and was later added to the specimen (F. Zachos. pers. comm.).

Unfortunately, we were not able to check the morphological characters diagnostic of *poecilotis* as we did with the type specimen of *D. albiventris*, since there is no skull associated with the specimen. It is noteworthy to mention that the ears of the type specimen of *D. poecilotis* are dark (**Fig**. 4), while the ears of *D. albiventris* s.l. are white and might have dark spots, which could indicate that the type specimen corresponds to *D. aurita*. Nonetheless, the description provided by Wagner mentions white ears (so it can be an effect of the aging of the specimen), and more importantly, the general coloration of the

Fig. 2. Type specimens of *Didelphis albiventris* ZMUC M02-CN4 and ZMUC M02-L4 (mounted specimen and cranium and postcranium, respectively), Natural History Museum of Denmark. Photographs are available on GBIF. https://www.gbif.org/occurrence/42778687

specimen with a white face with darker patches matches the coloration of *D. albiventris* s.l. The translation of the description of Wagner is as follows (the bold highlight is ours): *"Opossum with hair that is partly white and silky, some hairs are white at the base and black at the tip, while others (though very rarely) are entirely white; the head is white with narrow, triple stripes;* ***the ears are flesh-colored with white spots****. Its size is nearly equal to that of Didelphis cancrivora".* Examination of specimens housed at the Museu Nacional do Rio de Janeiro shows highly variable ear coloration, even in specimens from the same locality, with some showing completely skin-colored ears and others with mostly dark ears (João Oliveira pers.

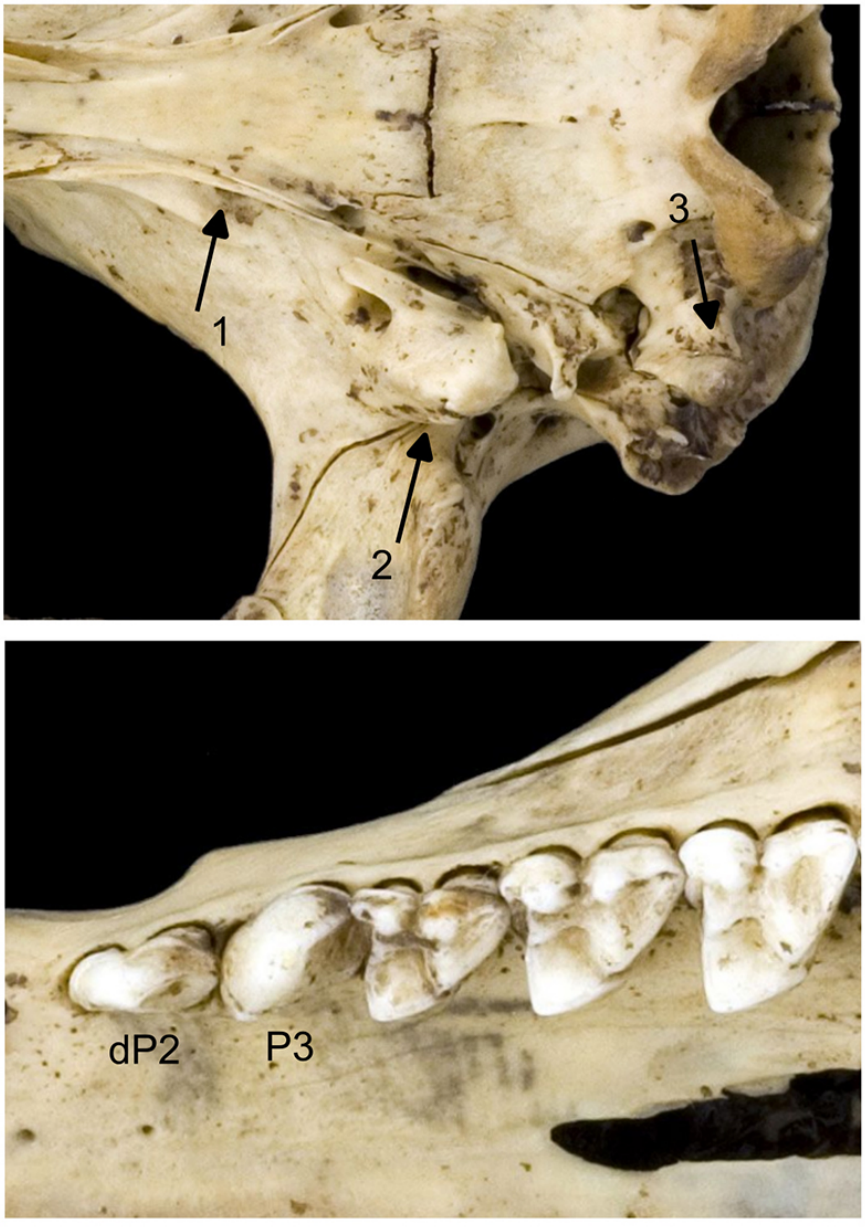

Fig. 3. Characters that differentiate *Didelphis albiventris* from *D. poecilotis* are observed on the type specimen. 1) Transverse sinus canal mostly hidden in ventral view; 2) alisphenoid portion of the bullae rounded and wide; 3) paracondylar process of the exoccipital straight and gracile; dP2: second upper premolar gracile, homogeneous in width without a broad talon; P3: talon of the third upper premolar (P3) not separated in two well-developed cingula.

comm.; see also Fig. S1). To avoid confusion with *D. aurita*, specimens of this species were also examined, showing a clearly yellow/orange coloration in the rostrum and completely dark ears. Also, the current distribution of *D. aurita* does not reach Mato Grosso, providing additional support to our identification as part of the southern group of *D. albiventris*.

Fig. 4. Type specimen of *Didelphis poecilotis* NMW ST 54 (mounted specimen), mammal collection of the Natural History Museum of Vienna. Photographs are courtesy of Frank Zachos.

The name of this southern form was originally published as *Didelphis poecilotus* by Wagner (1842) and later emended to *D. poecilotis* in 1847. The epithet *poecilotis* comes from a greek combination of words that mean spotted (poikilos) and ears (otis) and is in its female form, in agreement with the gender of *Didelphis* (Gardner 2005). Although Wagner (1847) did not write an explicit statement about the change in spelling, it can be considered justified because of the coincidence in gender between genus and specific epithet. Moreover, the name *D. poecilotis* was used subsequently by Wagner (1855) and by von Pelzeln (1883), who reviewed the species named after the specimens collected by Johann Natterer. Finally, it is important to note that Wagner (1842, 1847, 1855) attributed the name *Didelphis poecilotis* to J. Natterer, perhaps because it was the name given in the label of the specimen by Natterer or in his field books. Since it was Wagner who published the name, it should be attributed to him. If this is correct and the original name was given by Natterer, the correct author citation should be *D. poecilotis* Natterer in Wagner (1842), but we do not have enough evidence to use this citation since the original label is lost.

In Chemisquy et al. (2023), we mentioned that the putative name for the Southern group was *D. leucotis* Wagner, 1847 which is the name given to Azara's "Micouré premier" (Azara 1801) with the unknown type locality but coming from Paraguay or northeastern Argentina. However, *D. poecilotis*

has nomenclatural priority, and according to the proposed distribution for the southern species, individuals from Mato Grosso do not belong to *D. albiventris*.

The following text is an emended diagnosis for both species, a synonymy list, and their geographic distribution. Cursorial examination of skins from the type specimens and others preserved in museums show a high variation in color and coat pattern between northern and southern specimens, with no difference that allows a clear and unbiased identification. Therefore, in the diagnosis, there is no data on skin characteristics.

Didelphis albiventris Lund, 1840

Type locality: Rio das Velhas, Lagoa Santa, Minas Gerais, Brazil.
Type specimen: ZMUC M02-CN4 and ZMUC M02-L4 (mounted specimen and cranium and postcranium, respectively), Natural History Museum of Denmark.
Synonyms: none available.
Distribution: *Didelphis albiventris* occurs in central and northeastern Brazil, in the states of São Paulo, Paraná, Minas Gerais, Rio de Janeiro, Espirito Santo, Goiás, Tocantins, Bahía, Piauí, Ceará, Rio Grande do Norte, Paraiba, Pernambuco, Algoas, and Sergipe.

Emended diagnosis.
Cranium with a long distance between the postglenoid and posttympanic processes; straight and gracile paracondylar process of the exoccipital; rounded and broad alisphenoid portion of the bulla; long distance between the anterior portion of the alisphenoid and the rostral tympanic process of the petrosal; although variable in size, the transverse sinus canal is mostly hidden in ventral view. The upper teeth have a small and gracile second premolar, mostly homogenous in width (i.e., without a broad talon) and a poorly developed anterior cingulum; the talon of the third molar is not separated in two cingula by the posterior crest, but when present, the labial cingulum is very narrow and poorly developed; relatively small protocone with straight or less rounded postprotocrista; paracone and metacone closer (i.e., not clearly apart, especially in the second molar); absent cingulum between stylar cusp B and ectoflexus; relatively small paracone and metacone; and narrow parastylar region. In the lower teeth, the trigonid and talonid basins are similar in height; they have a relatively small anterobasal cingulum; a larger to subequal metaconid in relation to paraconid size; and in lateral view, the anterior cusp of the second premolar is located at the top 1/3 of the tooth, and the third premolar is short. The length of the first three upper and lower molars is 12.55 ± 1.32 mm and 12.36 ± 1.14 mm, respectively.

Didelphis poecilotis A. Wagner, 1842

Type locality: Cuiabá, Mato Grosso, Brazil.
Type specimen: NMW ST 54 (mounted specimen), mammal collection of the Naturhistorisches Museum Wien.
Synonyms: *Didelphis poecilonota* Schinz, 1844:504; incorrect subsequent spelling of *D. poecilotis*.
D. leucotis A. Wagner, 1847:127; based on Azara's Micouré Premier.
D. lechei Ihering, 1892:98; holotype BMNH 1891.3.20.9 from Rio Grande do Sul, Brazil.
Didelphys azarae antiqua Ameghino, 1889:278; holotype MLP 11-66 from the cliffs of the Rio Primero, Córdoba City, Argentina.
D. paraguayensis J. A. Allen, 1902:267; based on *Didelphis paraguayensis* Oken, 1816, which was based on Azara's Micouré Premier.
Didelphis paraguayensis bonariensis Marelli, 1930:2; "no type locality mentioned, range given as northeastern Argentina, including Buenos Aires; subsequently restricted to the provinces of Buenos Aires and Santa Fe by Marelli (1932:69)" (Cerqueira, & Tribe 2008).
Didelphis paraguayensis dennleri Marelli, 1930:2; "no type locality mentioned, range given as western Argentina, from Catamarca to southern Buenos Aires province; subsequently restricted to the province of Buenos Aires by Marelli (1932:69)" (Cerqueira, & Tribe 2008).
Note: Although the full name of Wagner was Johann Andreas Wagner, he signed his writings as A. Wagner, so the author must be cited that way, which is the current way of citing him in synonymy lists, and not as J. A. Wagner.
Distribution: *Didelphis poecilotis* occurs in Paraguay, Uruguay, southern Bolivia up to Cochabamba, throughout Argentina until the north of Patagonia, and in southwestern Brazil in the states of Rio Grande do Sul, Paraná, Santa Catarina, Mato Grosso do Sul, and Mato Grosso.

Emended craniodental diagnosis.
Cranium with a short distance between the postglenoid and posttympanic processes; posteriorly directed and robust paracondylar process of the exoccipital; compressed and narrow alisphenoid portion of the bulla; short distance between the anterior portion of the alisphenoid and the rostral

tympanic process of the petrosal; broad transverse sinus canal, which is clearly visible ventrally. The upper teeth have a large and robust second premolar, with a talon wider than the rest of the tooth and a well-developed anterior cingulum; the talon of the third molar is separated in two cingula, with a well-developed lingual cingulum and a narrow labial cingulum; a large and relatively well-developed protocone with rounded postprotocrista; well-separated paracone and metacone (especially in the second molar); presence of a cingulum between stylar cusp B and ectoflexus; large paracone and metacone; and relatively broad parastylar region due to a more lingually displaced paracone. Lower teeth have a trigonid clearly taller than the talonid; a well-developed anterobasal cingulum; a metaconid clearly larger than the paraconid; in lateral view, the anterior cusp of the second premolar is located in the middle of the tooth, and the third premolar is tall. The length of the first three upper and lower molars is 14.79 ± 1.115 mm and 14.16 ± 1.037 mm, respectively.

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